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CHROMOSOME NUMBER AND INDIVIDUALITY IN THE GENUS CREPIS

I. A COMPARATIVE STUDY OF THE CHROMOSOME NUMBER AND DIMENSIONS OF NINETEEN SPECIES

BY

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Because most of the species of the genus *Crepis* have low chromosome numbers, it offers obvious advantages for the study of comparative chromosome relations. The chromosome individuality of certain species is very distinct, so much so that it could be used as a diagnostic character in specific determination. These facts lead to an inquiry to discover first, whether upon careful analysis all species would prove to differ in chromosome individuality, and second, what relations the chromosome groupings of different species bear to one another. This question has been previously touched upon in several papers by Rosenberg (1909, 1918, 1920) and in a recent contribution by Marchal (1920). Rosenberg (1918) called attention to the fact that the genus *Crepis* possesses a great variety of chromosome numbers. His summary showed species with 3, 4, 5, 8, 9, and 20 pairs. In order to determine how such numerical differences had arisen within the genus, he measured the chromosomes of a three and a four-pair species, *capillaris* (*Reuteriana* of Rosenberg) and *tectorum*, respectively, and found, on the basis of measurements of homotypic anaphase chromosomes, that three of the chromosomes of the two species corresponded accurately in size and that the fourth pair of *tectorum* averaged slightly shorter than the shortest of *capillaris*. He noted that the two shortest chromosomes of *capillaris* often mate later than the other two in p.m.c. and finds associated with this fact a tendency toward lagging and irregular division. From these data he

concluded that the four-pair species have arisen from a three-pair species by the fusion of two gametes each of which has received an extra short chromosome. Although he did not publish measurements on the two five-pair species which he studied (*rubra* and *multicaulis*), he believed that both have three of the short chromosomes, and that these types have originated by a repetition of the process which gave rise to the four-pair types. In his 1920 contribution he changes his count in *biennis* from twenty to twenty-one pairs and concludes that it represents the three chromosomes of *capillaris* multiplied fourteen times.

Marchal, whose work was done without knowledge of Rosenberg's paper, expressed (1920) the belief that four is the ground number of the genus *Crepis*. He noted that p.m.c. of a slightly aberrant *capillaris* plant had what appeared to be a large quadrivalent multiple chromosome plus two smaller but equal elements, and that most of the species of *Crepis* seemed to have four pairs of chromosomes. He therefore concluded that *capillaris* had arisen from the type by end-to-end union between two chromosomes. He believed that the differences in length which had been noted for *C. lanceolata platyphylla* (Tahara and Ishikawa, 1911) could be accounted for by bipartition of one chromosome of a species with four pairs. He further suggested that six-pair species might arise by doubling of the three, and an eight-pair species by doubling of the four. He counted sixteen pairs for *biennis* and noted that, while the individual chromosomes in the p.m.c. of this species appeared somewhat smaller than those of certain four-chromosome species, the total mass was much greater. He then concluded that *biennis* is an eight-ploid species.

MATERIAL AND METHODS

A large number of species of the genus *Crepis* have been grown and identified in the greenhouse of the Division of Genetics of the University of California by Professor E. B. Babcock, thus making it possible to be certain of the specific determination of the material which was studied cytologically. Since the chromosome numbers which have been found to characterize the species thus identified differ in several instances from previously published counts, the data are presented in a convenient form in table 1. The root tips were fixed in chrom-acetic-urea and stained in Heidenhain's iron-haematoxylin. In most species the reduced number has also been counted by Belling's iron-aceto-carmine method.

TABLE 1

CHROMOSOME COUNTS OF 27 SPECIES OF CREPIS

Species	Number		Author
	N	2N	
alpina L.	4		Marchal (1920)*
		10	Rosenberg (1920)†
	5	10	Mann (1922)‡
amplexifolia Willk.	4	8	Mann
aspera L.	4		Marchal (1920)
	4	8	Mann (1922)
aurea (L.) Reichb.	5	10	Mann
biennis L.	16		Marchal (1920)
	20		Rosenberg (1918)
	21		Rosenberg (1920)
	20	40	Mann (1922)
blattarioides Vill.	4		Marchal (1920)
		8	Rosenberg (1920)
	4	8	Mann
breviflora Delile	4	8	Mann
bulbosa (L.) Tausch.	9	18	Mann
bursifolia L.	4	8	Mann
capillaris (L.) Wallr.	3	6	Rosenberg (1909), Mann (1922)
dioscoridis L.	4		Marchal (1920)
	4	8	Mann (1922)
foetida L.	4		Marchal (1920)
	4	8	Rosenberg (1918)
	5	10	Mann (1922)
grandiflora Tausch.	4	8	Mann
incarnata Tausch.	4	8	Mann
japonica (L.) Benth.	8	16	Tahara (1910), Mann (1922)
myriocephala Coss. et D. R.	4	8	Mann (1922)

* Marchal gives 1914 as the date of his counts, but they were not published until 1920.

† Figured but not mentioned in the text.

‡ Cited from Report of the College of Agriculture, University of California, July 1, 1921-June 30 1922.

TABLE 1—(*Continued*)

Species	Number		Author
	N	2N	
neglecta L.	4	8	Rosenberg (1918), Mann (1922)
palestina Boiss. Bornmüller	4	8	Mann
parviflora Desf.	4	8	Rosenberg (1918), Mann (1922)
pulchra L.	4	8	Rosenberg (1920), Mann (1922)
rubra L.	4		Marchal (1920)
	5	10	Rosenberg (1918), Mann (1922)
setosa Hall	4	8	Mann (1922)
sibirica L.	4		Marchal (1920)
	5	10	Mann (1922)
Sieberi Boiss.	6	12	Mann (1922)
taraxacifolia Thuill.	6	12	Beer (1912)
	4	8	Digby (1914), Mann (1922)
tectorum L.	4	8	Juel (1905), Mann (1922)
vesicaria L.	4	8	Mann

Table 1 shows that, while four is the most common haploid number for the twenty species studied, five is also fairly frequent. The other numbers (3, 6, 8, 9, and 20) are each represented by a single species. It is obvious that chromosome measurement should show whether cross-division, union into multiples, addition by non-disjunction, or combinations of these methods are sufficient to account for the differences in number found in the genus. It is also possible that hybridization between species with different chromosome numbers might account for the origin of certain cytological peculiarities.

For some species the cytological material is far more abundant than it is for others, so that it is possible to measure only somatic metaphases in which all the chromosomes are fairly straight. The tendency of the long chromosomes of *Crepis* to twist is a source of considerable error where relatively poor material is available. The finest metaphase figures are to be found in the upper portion of the rapidly growing region of the root in seedlings, and in roots from adult plants. The region containing fine figures is greater in roots from the latter than

in the short root of the cotyledon stage, because there is a longer growing area in which the cytoplasm is less dense than it is at the tip, so that the chromosomes spread out more freely and the picture is less obscured by cytoplasmic inclusions.

Table 3 is a compilation of measurement data for somatic metaphase figures in nineteen species of *Crepis*. In each case, except *japonica* and *sieberi*, ten somatic polar metaphases were drawn with a camera lucida. The magnification of the drawings is 4000 diameters. A moistened thread was placed along the center of the drawing of each chromosome, and then straightened and measured in millimeters. The figures were then placed in columns, the two largest in the first, and so on down to the two smallest. A sample of these records for a five-pair species, *alpina*, is given below in table 2.

TABLE 2

Actual Measurements of Drawings						Differences from Average				
1	2	3	4	5	Total Length	1	2	3	4	5
32 mm.	25 mm.	14 mm.	13.5mm.	13mm.						
31	27	14	13	12.5	195 mm.	+5.8	+5.7	−0.5	+0.4	+0.8
22.5	20	15.5	13	11.5						
24.5	18	14.5	13	11	163 mm.	−1.7	−1.3	+1.0	−0.1	−0.7
30.5	21	17	14.5	12.5						
22	19	15	14.5	13	179 mm.	+4.3	−0.3	+2.5	+1.4	+0.8
21.5	17	13	12	10.5						
23.5	19	13	12	11.5	153 mm.	−2.7	−2.3	−1.5	−1.1	−0.7
23	21.5	16.5	14	12						
29	20	15	12	11.5	174 mm.	+2.8	+0.2	+2.0	+0.9	−0.2

It is evident that even measurement by the rather crude method described above gives a fairly definite clue to the individuality of the species. It will also be noted that when the larger figure of each set is compared with the average for the chromosome, obtained by dividing the sum of the ten larger of the twenty chromosomes of one type by ten, the deviations for any one metaphase set are generally in the same direction (+ or −). (See column headed "Differences from the average.") This deviation indicates that the error of measurement was not sufficient to conceal the fact that the chromosome lengths of a species maintain certain size relations at least throughout the later periods of shortening. It also shows that it is fair to use an average

so obtained in a comparative study like this. The larger figure of each set was considered the more accurate measurement and hence was used to secure the 'corrected' totals and averages which appear in table 3.

TABLE 3

MEASUREMENT DATA FOR NINETEEN SPECIES OF CREPIS

Species	Haploid chromosome number	Corrected average total length	Corrected average for individual chromosomes								
C. capillaris	3	61.4	26.2	20.4	14.8						
C. neglecta	4	61.7	24.5	16.2	11.2	9.8					
C. setosa	4	63.2	22.3	17.8	14.0	9.1					
C. parviflora	4	69.9	25.3	20.5	14.4	9.7					
C. bursifolia	4	78.5	24.3	22.0	19.5	12.7					
C. aurea	5	83.5	21.0	18.0	16.2	15.1	13.2				
C. aspera	4	82.6	23.9	21.5	19.7	17.5					
C. alpina	5	87.3	26.2	21.3	14.5	13.1	12.2				
C. taraxacifolia	4	88.4	26.1	23.3	21.2	17.8					
C. tectorum	4	88.7	28.1	23.2	20.2	17.2					
C. blattarioides	4	91.1	29.0	23.8	20.6	17.7					
C. japonica [a]	8	92.6	15.7	13.5	12.2	11.5	10.8	10.0	9.7	9.2	
C. foetida	5	93.7	25.0	20.8	17.7	15.8	14.4				
C. bulbosa	9	100.5	13.9	12.8	12.1	11.7	11.1	10.6	10.1	9.6	8.6
C. rubra	5	102.9	29.4	23.9	18.5	16.2	14.9				
C. dioscoridis	4	109.4	35.9	29.3	24.9	19.3					
C. sieberi [a]	6	109.6	26.8	21.4	17.7	16.0	15.2	12.5			
C. pulchra	4	112.1	36.7	30.6	25.5	19.3					
C. sibirica	5	143.6	41.9	32.4	27.6	23.2	18.5				

[a] Averages from less than ten figures.

The reliability of such measurements and the evidence for the constancy of specific individuality have been further corroborated by a study of chromosome measurements of the F_1's of two species-hybrids, *setosa*×*tectorum* (fig. 1) and *setosa*×*dioscoridis* (fig. 2).[1] It will be noted from table 3 that all three species involved have four pairs and that the chromosome sizes are far more different in the two latter than in the two former species. In both F_1's, however, it was possible to determine the source of the chromosomes by means of measurement data, and this was facilitated by the peculiar semidetached tip of the longest chromosome of *setosa* (fig. 3), by which it may usually be identified. Since only one member of a set is present in each F_1 figure, it seemed best to compare the averages for the F_1's with the uncorrected averages for the species involved. The results are tabulated below:

[1] For the use of these hybrids and the data on hybridization given below, I am indebted to Dr. J. L. Collins of this laboratory.

TABLE 4

setosa×*dioscoridis*	39.9	33.6	28.9	23.1	22.1	18.1	13.7	10.3
setosa					22.3	17.8	14.0	9.1
dioscoridis	34.2	28.9	24.9	20.6				
	+5.7	+4.7	+4.0	+2.5	−0.2	+0.3	−0.3	+1.2
setosa×*tectorum*	29.4	24.1	21.2	16.8	21.0	18.9	13.3	8.9
setosa					22.3	17.8	14.0	9.1
tectorum	28.1	23.2	20.2	17.2				
	+1.3	+0.9	+1.0	−0.4	−1.3	+1.1	−0.7	−0.2

The important point is that one can identify the chromosomes of *dioscoridis* and of *tectorum* by measurement when they are in combination with those of *setosa* in an F_1 hybrid, so that it is evident that the specific differences in length noted are not the product of interaction between a certain cytoplasm and its chromosomes.

Since abundant material was available for *capillaris* (fig. 6), the first measurements, which were made on ten figures about as good as the average for all species, were checked by the use, first, of a mixture of slightly different metaphase stages (beginning to almost complete division) from a very short region of a single root tip, and, second, of a mixture from undivided figures from two different roots. These measurements show that averages for one chromosome in three different sets of ten from the same species may differ by as much as 3.55 mm., but that the averages give, in each case, very nearly the same differences between the lengths of the different pairs.

COMPARISON OF SPECIES

Crepis neglecta (fig. 7) has a very characteristic individuality, two of the pairs being very similar and distinctly shorter than any of the chromosomes of *capillaris*. Its total length is very similar to that of *capillaris*, so much so that one is inclined to test the cross-division hypothesis for this species. If the two shortest averages are added, their sum is practically the same as the average for the intermediate chromosome of *capillaris* and the other average lengths are very similar.

capillaris	26.2		20.4	14.8
neglecta	24.5	11.2+9.8=21.0		16.2
	−1.7		+0.6	+1.4

Attempts to cross the two species have as yet been unsuccessful.

Setosa (fig. 3), like *neglecta*, differs little from *capillaris* in total length. It contains, however, only one pair of chromosomes shorter than any in *capillaris;* otherwise it is rather similar to it.

capillaris	26.2	20.4	14.8	
setosa	22.3	17.8	14.0	9.1
	−3.9	−2.6	−0.8	+9.1

It has already been noted that the longest chromosome of *setosa* has a semidetached tip by which it may be recognized. This tip is usually at an angle to the main portion of the chromosome. In the figures given above the longest chromosome of *setosa* appears to have lost a portion of its length, while another pair of chromosomes averaging about ten units has been added. It is also possible that the longest chromosome has cross-divided, and that the peculiar chromosome of *setosa* really corresponds to the intermediate of *capillaris*.

capillaris	26.2	20.4	14.8
setosa	17.8+9.1=26.9	22.3	14.0
	+0.7	+1.9	−0.8

If either of these possibilities represented the whole truth concerning the difference between the two species, we should expect reduction to be fairly normal following hybridization. As a matter of fact, *no pairing occurs* in the F_1 *setosa* (N=4)×*capillaris* (N=3) (Collins and Mann, 1923), and as a consequence gametes are formed with 3, 4, and 6 chromosomes as shown by five plants (backcrosses to *setosa*), which have 7, 8, and 10 somatic chromosomes. It seems possible that new types differing in number and combination of chromosomes may be obtained by selfing such plants as the backcrosses with ten chromosomes.

Crepis parviflora (fig. 8) has a chromosome individuality much like that of *setosa;* the longer chromosome, however, averages slightly longer and does not appear to have a semidetached tip.

setosa	22.3	17.8	14.0	9.0
parviflora	25.3	20.5	14.4	9.7
	+3.0	+2.7	+0.4	+0.7

It is evident that *parviflora* is more similar to *capillaris* than *setosa*, but like *setosa* it has an additional short pair of chromosomes.

capillaris	26.2	20.4	14.8	
parviflora	25.3	20.5	14.4	9.7
	−0.9	+0.1	−0.4	+9.7

The first hypothesis for *setosa* appears to be the more probable for *parviflora*. If it were true, one would have to account for the additional chromosome of 9.7 units by hybridization between two such forms as

neglecta and *capillaris*. The hybridization results for *setosa*×*capillaris* given above indicate that new types with new combinations of chromosomes may arise in this manner. It will be interesting to observe the results of crossing *setosa* and *parviflora*.

Bursifolia (fig. 9) appears to have an extra element of the size of the intermediate chromosome of the *capillaris* series:

capillaris	26.2		20.4	14.8
bursifolia	24.3	$\frac{22+19.5}{2}=20.7$		12.7
	−1.9		+0.3	−2.1

It's average total length is 17.1 units longer than that of *capillaris*.

Crepis taraxacifolia (fig. 10), *tectorum* (fig. 5), and *blattarioides* (fig. 11) have very similar chromosome groups.

taraxacifolia	26.1	23.3	21.2	17.8
blattarioides	29.0	23.8	20.6	17.7
tectorum	28.1	23.2	20.2	17.2

All the chromosomes of these three species tend to average slightly larger than those of *capillaris*, but the differences do not greatly exceed those of the different averages for *capillaris*. If we suppose that the intermediate chromosome of *capillaris* has been duplicated in this group of species, the correspondence is somewhat bettered.

Average of *taraxacifolia*, *tectorum*, and *blattarioides*	27.7	22.05	17.6
Average of *capillaris*	26.2	20.40	14.8
	+1.5	+1.65	+2.8

It is obvious that the relative lengths of the chromosomes in these three species are very similar to those in *capillaris*.

Tectorum and *capillaris* were repeatedly crossed by Collins (1920), but the F_1 developed only as far as the cotyledon stage. This indicates an incompatibility of the chromosomes or cytoplasm hard to account for on the basis of mere addition of similar material, especially when one considers that trisomic forms which come to maturity appear to be not uncommon among plants and animals. It will be very interesting to know whether others of the group of species indicated above will behave like *tectorum* in crosses with *capillaris*, and whether they will intercross.

Aspera (fig. 12) is like the group discussed above except that the longest chromosome appears to be rather short.

capillaris	26.2		20.4	14.8
aspera	23.9	$\frac{21.5+19.7}{2}=20.6$		17.5
	−2.3		+0.2	+2.7

Crepis bursifolia, taraxacifolia, tectorum, blattarioides, and *aspera* might all be derived from *capillaris* by duplication of the intermediate pair of chromosomes.

The five-pair species listed below, although generally rather similar in chromosome individuality, show certain distinct differences.

							Total length
aurea		21.0	18.0	16.2	15.1	13.2	161.9
alpina	26.2	21.3	14.5	13.1	12.2		174.6
foetida	25.0	20.8	17.7	15.8	14.4		187.4
rubra	29.4	23.9	18.5	16.2	14.9		205.8

Aurea (fig. 13) is outstanding since it lacks a long chromosome of about twenty-five units. The figures are excellent, so that the averages must be considered as very nearly accurate. *Aurea* is also very distinctive morphologically. *Alpina* (fig. 14), *foetida* (fig. 15), and *rubra* (fig. 16) are much more alike in chromosome individuality. *Alpina* seems to have three pairs resembling the shortest chromosome of *capillaris*, and to be cytologically very like it otherwise.

capillaris	26.2	20.4	14.8
alpina	26.2	21.3	$\frac{14.5+13.1+12.2}{3}=13.2$
	0	+0.9	−1.6

Foetida might also have three duplicates of the shortest chromosome of *capillaris*.

capillaris	26.2	20.4	14.8
foetida	25.0	20.8	$\frac{17.7+15.8+14.4}{3}=15.9$
	−1.2	+0.4	+1.1

The figures for *rubra* compare better with those of *capillaris* if we average the two intermediates and the two shortest together.

capillaris	26.2	20.4	14.8
rubra	29.4	$\frac{23.9+18.5}{2}=21.2$	$\frac{16.2+14.9}{2}=15.5$
	+3.2	+0.8	+0.7

It was noted above that Rosenberg (1918) suggested that probably the small chromosome of *capillaris* had been duplicated twice for *rubra*. It will be seen from the figures that duplication of the intermediate and of the short chromosome appears more probable on the basis of the measurements presented here.

Crepis japonica (N=8) (fig. 17) and *bulbosa* (N=9) (fig. 18) are rather similar in chromosome individuality, but are totally different from all the rest of the species studied in chromosome number and size.

japonica	15.7	13.5	12.2	11.5	10.8	10.0	9.7	9.2	
bulbosa	13.9	12.8	12.1	11.7	11.1	10.6	10.1	9.6	8.6

It is, of course, possible that *japonica* might have been derived from a species like *tectorum* by cross-division of every chromosome, or vice versa. When we test this hypothesis by adding the averages for the two largest, the next two, etc., of *japonica* together, the results are rather striking.

japonica	15.7	12.2	10.8	9.7
	13.5	11.5	10.0	9.2
	29.2	23.7	20.8	18.9
tectorum	28.1	23.2	20.2	17.2
	+1.1	+0.5	+0.6	+1.7

It is at least obvious that tetraploidy could not explain the chromosome individuality of *japonica* while cross-division might do so.

Crepis sieberi (fig. 19) is the only species so far studied which has six pairs of chromosomes. It looks as if it might have four pairs of short chromosomes:

capillaris	26.2	20.4		14.8
sieberi	26.8	21.4	$\frac{17.7+16+15.2+12.5}{4}=15.3$	
	+0.6	+1.0		+0.5

or two intermediate and three short pairs:

capillaris	26.2		20.4		14.8
sieberi	26.8	$\frac{21.4+17.7}{2}=19.5$		$\frac{16+15.2+12.5}{3}=14.6$	
	+0.6		−0.9		−0.2

Crepis pulchra (fig. 21) and *dioscoridis* (fig. 4) are very similar to one another in chromosome length.

pulchra	36.7	30.6	25.5	19.3
dioscoridis	35.9	29.3	24.9	19.3
Difference	0.8	1.3	0.6	0

C. sibirica (fig. 23), with five pairs, resembles *pulchra* and *dioscoridis* in choromosome measurements, and the average length of the two longest chromosomes, 36.5, indicates that it may have two instead of one of the longest type of chromosome.

sibirica	$\frac{41.9+32.4}{2}=37.1$	27.6	23.2	18.5
dioscoridis	35.9	29.3	24.9	19.3
Difference	1.2	1.7	1.7	0.8

If we suppose that this group of species has been derived from a type like *capillaris*, we must consider that the longest chromosome represents a multiple. If we subtract the intermediate average for *capillaris* (20.4) from the average of the longest chromosomes of all three species in this group (36.3), the remainder, 15.9, is only 1.1 units longer than the shortest chromosome of *capillaris*, indicating that an intermediate and a short chromosome might have united end to end to form an element averaging 36.3 units. Then if we average the two shortest chromosomes of these three species with the chromosome of 20.4 units, which, we have supposed has united with a short element, the average, 19.9, is so like the intermediate of *capillaris* as to suggest that it may have been duplicated in the group under consideration. When we look at the averages now, the figures compare very well.

capillaris		26.2	20.4	14.8
pulchra, dioscoridis, and *sibirica*	$\frac{30.6+29.3+27.6}{3}=29.1$	19.9	15.9	
		+2.9	−0.5	+1.1

These species obviously form a group by themselves, especially since it has been shown that the great size of the chromosomes in *dioscoridis* is maintained upon hybridization with a species like *setosa*.

DISCUSSION

For two reasons it is impossible to make any sweeping generalizations at this time concerning the data presented here. First, we do not yet know how *species* differing in chromosome number can arise, and second, we know too little about the genetics of *Crepis*. There are two known methods by which a single pair of chromosomes can be added to a complex, non-disjunction and species-hybridization, but in neither case has it been proved that *stable types* would ever result; and the formation of new species presupposes stability. It has been suggested that it is very improbable that stability is to be expected of tetrasomic individuals because the complex as a whole is unbalanced by the addition of chromosomes. This view seems to be borne out by observations on the cytology of tetrasomic plants of *Datura* (Belling and Blakeslee,

1924) and *Matthiola* (Frost and Mann, 1924). Both of these tetrasomic types are even feebler than the trisomic plants, and hence would have little chance of survival under unfavorable environmental conditions. The possibilities of species-hybridization as a source of differences in chromosome number within a genus are still less known. It might be argued with some plausibility that if a tetrasomic condition is unbalancing and associated with lessened viability, even less in the way of stability and viability should be expected of organisms having a pair of chromosomes from another species added to a complete specific complex. The *Drosophila* workers have found, however (Morgan, 1922), that a similar genic structure characterizes the chromosomes of several species of that genus, and if this is true of *Crepis*, one method may be as probable as the other. It has been shown (Collins and Mann, 1923) that new types with more chromosomes than either species possesses are formed when the F_1 *C. setosa*×*C. capillaris* is backcrossed to *setosa*. It is only through further work on such types that the question of stability can be answered. The theoretical and practical value of such work is self-evident.

While the little work that has so far been done on tetrasomic plants tends to show that they would be expected to be somewhat unstable genetically, tetraploid plants, e. g., *Oenothera gigas*, breed true. That *Crepis biennis* may be an octaploid from a five-pair species is indicated by the following experimental evidence:

1. In the F_1 *C. setosa*×*C. biennis* the twenty pairs of chromosomes from *biennis* form *ten* pairs.

2. In the backcross of this F_1 to *biennis* the thirty chromosomes from *C. biennis* form fifteen pairs.

The great size and vigor which distinguish it from the other species studied also indicate that it is polyploid. The evidence from chromosome measurements indicates strongly that *Crepis biennis* is the only one of the twenty species discussed in this paper that could owe its origin to polyploidy.

It would seem possible that, if the whole complex of one species were added to that of another by segregation following species-hybridization, zygotes formed by the union of two such gametes might be expected to give stable races differing in chromosome number from other species of the genus. There is no evidence that such a procedure has occurred in any of the species of *Crepis* discussed above.

There is at present little evidence that whole chromosomes can be lost and the resulting organisms be expected to give rise to new species. Genetical and cytological results on *Drosophila* (Bridges, 1921) indicate

that while 53 per cent of the expected flies lacking one of the small fourth chromosomes live, they are imperfect, weak, and often sterile. That a small portion of a chromosome may be lost or inactivated is indicated also by work on this fly (Bridges, 1919). Loss of this strain is attributed to the injurious effect of the deficiency upon viability, fertility, and productivity.

While loss of chromosomes appears to be somewhat improbable as a method by which one species can come to differ from another in chromosome number, the chromosome number of some species may be reduced as a result of permanent end-to-end union of certain chromosomes to form multiples. The differences in number noted for the *Acrididae* (McClung, 1917) appear to be of this type. One species, *Hesperotettix viridis*, shows considerable variation in chromosome union in different individuals, indicating that it may be in the process of producing new types of chromosome grouping. It is also decidedly variable morphologically.

There is some observational evidence that species differ from one another in chromosome number due to cross-division of all chromosomes of a complex. Marchal (1920), for example, reported that in the section Medium of *Campanula* the size of each chromosome of pollen mother cells is less when the haploid specific number is thirty-four than when it is seventeen.

It is difficult to understand how cross-division or union of chromosomes to form multiples could *cause* specific differences. In fact, a case from *Drosophila* reported by Mrs. Morgan (1922) indicates that while end-to-end union of the X-chromosomes may affect genetic results it has no effect upon specific characters. It seems simpler to suppose that such changes in chromosome complexes are the result rather than the cause of genetical differences between individuals, such as have been noted for *Hesperotettix viridis* and for the different species of the Acrididae.

In the genus *Drosophila*, it has been shown that chromosomes that look alike may carry very different genes. For example, in *D. willistoni*, Metz and Lancefield (1922) report that the X-chromosome is a V-shaped element similar to the second and third autosomes of *D. melanogaster*. Without this genetic evidence one would have said that these two species had the same type of chromosome complex. Such evidence is a timely warning to those who would draw hasty conclusions on the basis of data like those given above for *Crepis*. The genetical results from *Crepis* are still too scanty to permit of such tests.

SUMMARY AND CONCLUSIONS

1. With the exception of *neglecta* and possibly *setosa*, all the species of *Crepis* studied show significant increases in total length of the chromosome complex over that of *capillaris*, the single species with three pairs of chromosomes.

2. Generally speaking, increased number is associated with increased total length, but there are certain exceptions.

3. In so far as studies on chromosome individuality can determine, five of the species with four pairs of chromosomes might have two pairs like the intermediate chromosome of *capillaris*.

4. In *Crepis neglecta* (N = 4) the two shortest chromosomes might have been derived by cross-division of a chromosome of the length of the intermediate chromosome of *capillaris*.

5. *Crepis setosa* (N = 4) and *parviflora* (N = 4) are very similar in total length and quite unlike all of the other species.

6. *Crepis dioscoridis* (N = 4) and *pulchra* (N = 4) have a long pair of chromosomes which is not represented in *capillaris* or in the other four chromosome species. It is possible that it might be a multiple chromosome. That this difference in length is not due to a difference in physiological condition or to error is shown by the fact that it is maintained when the *dioscoridis* chromosomes are in *setosa* cytoplasm in an F_1 between these two species. All the chromosomes of these two species can be distinguished in this F_1.

7. *Aurea* stands out among the species with five pairs because of its lack of an element like the longest chromosome of *capillaris*. The complexes of *rubra*, *foetida*, and *alpina* might all have been derived by duplication of certain chromosomes of *capillaris*. *Sibirica* seems to possess two chromosomes like the large element of *dioscoridis* and *pulchra*.

8. The single species with six pairs, *sieberi*, has chromosomes which are enough like those of *capillaris* in length to have been derived from it by chromosomal duplication. There appear to be but one pair of the large and the intermediate types, and four pairs like the short chromosomes.

9. *Japonica* with eight pairs might be derived by cross-division of all chromosomes of a species like *tectorum*.

10. *Bulbosa* (N = 9) has short chromosomes like those of *japonica*.

11. *Biennis* (N=20) has chromosomes comparable in size to those of *capillaris*, and there is some experimental evidence which indicates that it is a polyploid from a five-pair species.

12. It is well understood that these data are simply suggestive, but it is hoped that they may be of some use in taxonomic and hybridization studies on *Crepis*. The evidence, based on especially favorable cytological material, shows that it is entirely unsafe to assume that even closely related species which have the same chromosome numbers are identical in chromosome individuality; or to assume polyploidy unless the sizes of the chromosomes have been compared.

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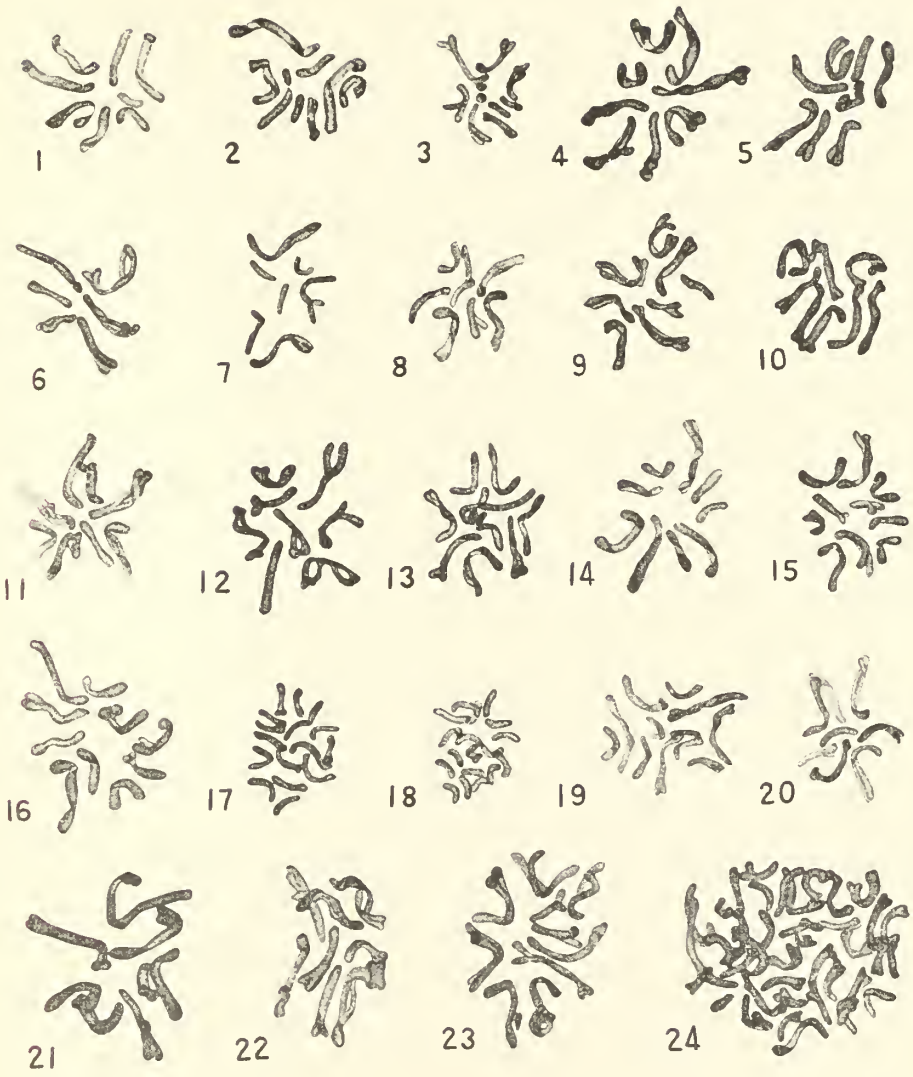
PLATE 53

Somatic metaphases of *Crepis* species magnified 4000 diameters, using a B. and L. camera lucida mirror at 50, bar at 110, and a 1.8 mm. oil objective with an 18X Zeiss compensating ocular. Reduced in reproduction to 1800 diameters.

1. F_1 *setosa*×*tectorum*
2. F_1 *setosa*×*dioscoridis*
3. *setosa*
4. *dioscoridis*
5. *tectorum*
6. *capillaris*
7. *neglecta*
8. *parviflora*
9. *bursifolia*
10. *taraxacifolia*
11. *blattarioides*
12. *aspera*
13. *aurea*
14. *alpina*
15. *foetida*
16. *rubra*
17. *japonica*
18. *bulbosa*
19. *sieberi*
20. *amplexifolia*
21. *pulchra*
22. *grandifolia*
23. *sibirica*
24. *biennis*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CHROMOSOME NUMBER AND INDIVIDUALITY IN THE GENUS CREPIS

II. THE CHROMOSOMES AND TAXONOMIC RELATIONSHIPS

BY

ERNEST BROWN BABCOCK AND MARGARET MANN LESLEY

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INTRODUCTION

For the past three years we have been accumulating data on the taxonomy and cytology of the genus *Crepis*. The present paper represents only two phases of our general project, which also includes extensive genetic research on species and species hybrids, the whole undertaking being an effort to establish a natural classification of a genus which has been a source of considerable difficulty to taxonomists and which presents a wide array of chromosome numbers. In addition to number we have examined the size of the chromosomes in the species studied, in the hope that this might also prove useful as a criterion in classification.

We are confining our discussion to species which we have been able to cultivate in the greenhouse or garden and to identify with certainty, a procedure which has thrown considerable light on the classification. Ideally the taxonomist should know his species as they appear under natural conditions, but obviously this is impossible for any one botanist in the case of such a large and widely distributed genus as *Crepis*.

But, even though field studies of most of the species could not be made, it was yet necessary to cultivate them in order to study them cytologically, and hence it has been possible to supplement the examination of herbarium material by observations on cultivated plants which were grown under fairly uniform conditions. By this method it has been possible to show that certain characters (for example, nodding position of the young flower heads) which have been used by some authors to separate sections of the genus, are variable within a single species.

Crepis was chosen in the first place because certain species have small chromosome numbers and because the chromosomes are comparatively easy to study in some detail. A previous paper on chromosome size and number in the genus (Mann, 1925) contained a majority of the chromosome data herein considered, together with a suggestion as to how a cytologist would be tempted to group the species studied. In this paper we have added somewhat to the cytological data and have attempted to utilize both the cytological and the taxonomical modes of attack. Generally speaking, this method has proved of the greatest usefulness; and, while certain irreconcilable situations still appear to exist, we have reason to hope that future developments—as we obtain more species and make further studies—may show how such situations have arisen and lead the way to a clearer understanding of the genus.

MATERIAL AND METHODS

The species of *Crepis* upon which this study is based are all from the Old World, and have mostly been obtained through the coöperation of European botanists. Since we desire to make our study as complete as possible, we shall greatly appreciate any assistance towards obtaining viable seeds or roots of additional species. The taxonomic studies have included the examination of both dried and living specimens, and much care has been exercised in the determination of all this material. The cytological methods were described in Mann (1925).

Acknowledgments

The investigations herein reported were conducted in part through an allotment from the Adams Fund. It is with pleasure that we acknowledge the assistance of Dr. J. L. Collins and Mr. C. W. Haney in the growing of cultures and in providing us with certain data on species hybridization. All the drawings were made by Helen E. Rearwin, whose attention to accuracy of detail is gladly acknowledged. Our thanks are also due to the curators of herbaria and directors of

botanic gardens in numerous institutions. Many taxonomic and other treatises on the Compositae have been consulted, which cannot be cited in this brief paper.

TAXONOMY AND CYTOLOGY OF TWENTY-ONE SPECIES OF CREPIS

In the present paper we do not wish to discuss the taxonomy of *Crepis* in detail or to propose any taxonomic revision of the genus, but merely to set forth the general features of the group and its subdivisions in such a way as to enable the reader to appreciate some of the difficulties involved in attempting to classify the species according to a natural system. Also, it is hoped that the significance of the cytological data herein presented will be clearer after a preliminary consideration of the outstanding morphological resemblances and differences to be found within this group of plants.

No thoronghgoing investigation of the entire genus has been made. Some of the species have been studied since the time of Linnaeus or even earlier, and at least forty-four other generic names have been applied by twenty-four authors in attempting to classify various portions of the assemblage. The purposes of the present paper can be best served by a discussion of the treatment of the genus given by Hoffmann in Engler and Prantl's Pflanzenfamilien. This treatment, represented in condensed form below, includes all but six of the twenty-one species for which complete data as to chromosome size are available and one other (*C. patula*) which we have not yet been able to secure. The six species referred to—*blattarioides* Vill., *bursifolia* L., *neglecta* L., *parviflora* Desf., *montana* d'Urville, and *setosa* Hall. f.—are all easily placed in Hoffmann's categories with the exception of *neglecta*, which is referred to **Eucrepis** in most recent floras (see p. 327). A translation of Hoffmann's description of the genus is given below for the information of readers who are not familiar with this groups of plants. His analysis of the genus and key to the sections appear in table 1.

Crepis L.—Heads small to rather large, yellow- or seldom red-flowered, borne singly or in panicles of variable form; involucre cylindrical or bell-shaped, often with loose or appressed outer calyx, the inner fructiferous bracts often becoming stouter and harder throughout or along the middle nerve; receptacle naked or ciliate; fruit 10–30 ribbed, with a short callosity on the base, reduced or beaked at the apex, the outer fruits sometimes shaped differently from the inner ones; pappus in most species composed of soft pliable hairs, seldom somewhat brittle and brownish, in the marginal fruits sometimes lacking.—Herbs, very seldom half-shrubby plants. Perhaps 170 species mostly from the northern hemisphere.

Fig. 1. Achenes of *Crepis alpina*—*a*, marginal; *a'*, inner. × 7 *circa*.

Fig. 2. Marginal and inner achenes of: *b*, *b′*, *Crepis rubra*; *c*, *c′*, *C. foetida*. × 7 *circa*.

TABLE 1

HOFFMANN'S KEY TO THE SECTIONS OF *Crepis* WITH THE ADDITION OF SIX SPECIES NOT LISTED BY HIM AND REFERENCES TO ORIGINAL DRAWINGS OF ACHENES

A. Pappus bristles very short, unequal, the longest scarcely as long as the width of the fruit, very readily deciduous; fruit short-beaked.

Sec. I. **Ceramiocephalum** Schultz Bip.*
C. patula Poir.

B. Pappus bristles longer.

(*a*) Inner or all the fruits long-beaked.

Sec. II. **Barkhausia** Mnch.*
Fruits all beaked (outer sometimes shorter than inner), involucre mostly with outer calyx, seldom imbricate. Fig. 1, *a*, *a'*; Fig. 3, *d*, *e*, *e' g*, *g'*.
C. alpina L., *taraxacifolia* Thuill., *bursifolia* L., *setosa* Hall. f.

Sec. III. **Anisoderis** Cass.*
Outer fruits short-, inner long-beaked. Fig. 2, *b*, *b'*, *c*, *c'*.
C. foetida L., *rubra* L.

Sec. IV. **Nemauchenes** Cass* (in part).
Marginal fruits not or scarcely beaked, enclosed within the much hardened involucral bracts; ribs prominent, the innermost enlarged wing-like so the fruits seem to be compressed; inner fruits prismatic long-beaked. Fig. 3, *h*, *h'*.
C. aspera L.

(*b*) Fruits reduced at the apex, but not beaked or only short-beaked.

Sec. V. **Nemauchenes** Cass.* (in part).
Except for the scarcely beaked inner fruits, like IV. Fig. 4, *k*, *k'*.
C. Dioscoridis L.

Sec. VI. **Cymboseris** Boiss.*
Marginal fruits compressed, 3-angled, the edges winged, enclosed by the inner much hardened involucral bracts, without pappus. Fig. 4, *m*, *m'*, *m''*.
C. *palaestina* Boiss. (Bornm.).

Sec. VII. **Phaecasium** Cass.*
Fruits alike in shape with readily deciduous pappus which is mostly absent in the marginal fruits, inner fructiferous involucral bracts much hardened. Fig. 4, *n*, *n'*, *n''*.
C. pulchra L.

Sec. VIII. **Aetheorrhiza** Cass.*
Distinct from others by tuberous root-stock, fruits all similar in shape. Fig. 6, *u*.
C. bulbosa (L) Tausch.

Sec. IX. **Eucrepis** DC.
Roots not tuberous (fusiform or root-stock as though bitten off); fruits all alike; involucre with outer calyx; inner fructiferous involucral bracts mostly moderately thickened. Fig. 5, *o*, *p*, *q*, *r*, *s*, *t*.
C. capillaris (L) Wallr., *neglecta* L., *parviflora* Desf., *tectorum* L., *biennis* L., *montana* d'Urv.

* Described as a genus.

Sec. X. **Youngia** Cass.*

Distinct from preceding section in the small few-flowered (8–15) heads. Stem few-leaved; involucre in mature fertile heads little changed. Pappus readily deciduous. Fig. 6, *v*, *v'*.

C. japonica (L) Benth.

Sec. XI. **Catonia** Much.*

Involucre imbricate, often black hairy; outer bracts shorter but at least half as long as inner bracts and forming no distinct outer calyx, in mature fertile heads flat and unchanged. Fig. 6, *w*, *x*,; fig. 7, *y*.

C. sibirica L., *aurea* (L) Cass., *blattarioides* Vill.

We shall first discuss Hoffmann's grouping of the twenty-one species now before us, and then suggest a more natural grouping, in order that the cytologic data to be presented may be more intelligently considered. It will be noted that the genus, as treated by Hoffmann, is divided into three subgenera but without designating them as such. The first consists of the monotypic section, **Ceramiocephalum**; the second (*a*) contains three sections all characterized by having fruits with definite beaks; and the third (*b*), comprising the remaining seven sections, contains species none of which have manifestly beaked fruits. It was long ago pointed out (Bischoff, 1851) that all degrees of development of the beak are found in group (*a*), while some of the species included in group (*b*) have fruits with very short or obscurely developed beaks. But this seems to be generally looked upon as merely part of the evidence of relationship within the whole group and as part of the argument for treating it as a single genus.

Section I is set apart from all the other species, probably justifiably, but as we have not yet been able to work with living material of this interesting species, it is unnecessary to give it further consideration at present.

Subgenus (*a*), on the basis of fruit characters alone, would be better rearranged as follows:

Sec. II. Fruits large, the inner ones 10–18 mm. long.
C. alpina, *foetida rubra* (cf. figs. 1 and 2).
Sec. III. Fruits small, all alike, the inner ones 5–8 mm. long.
C. bursifolia, *setosa*, *taraxacifolia* (cf. fig. 3, *d*, *e*, *g*).
Sec. IV. Fruits small, of two shapes, marginal ones winged.
C. aspera (cf. fig. 3, *h*, *h'*).

Furthermore, the above rearrangement is not inconsistent with other morphological characters of diagnostic value. This is especially interesting in connection with the cytological evidence, the species

* Described as a genus.

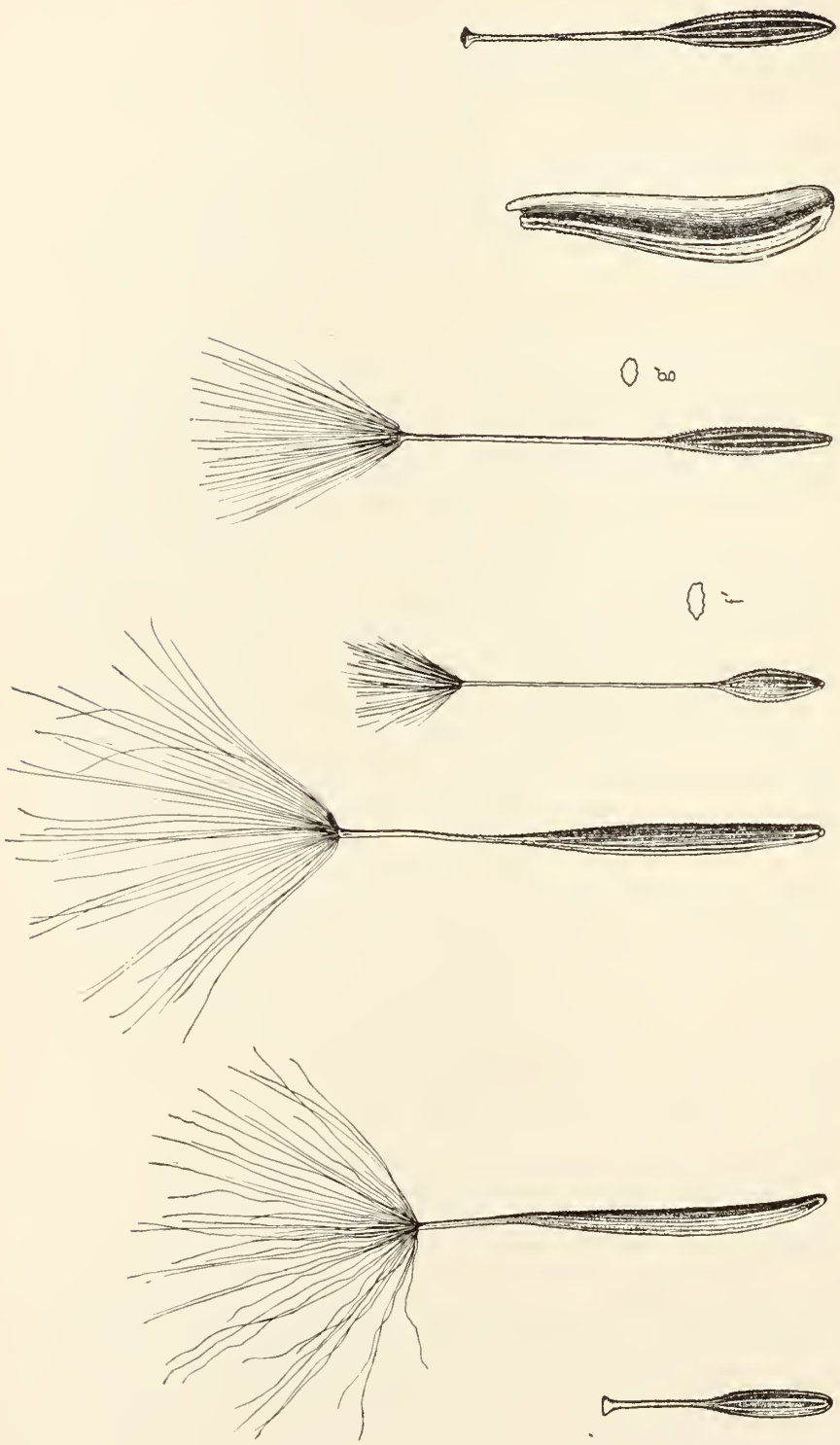

Fig. 3, *d*, typical achene of *Crepis setosa*; *e*, *e'*, marginal and inner achenes of *C. taraxacifolia*; *f*, typical achene of *C. senecioides*, *f'*, outline of cross-section of same; *g*, typical achene of *C. bursifolia*; *g'*, outline of cross-section of same; *h*, *h'* marginal and inner achenes of *C. aspera*. × 7.5 *circa*.

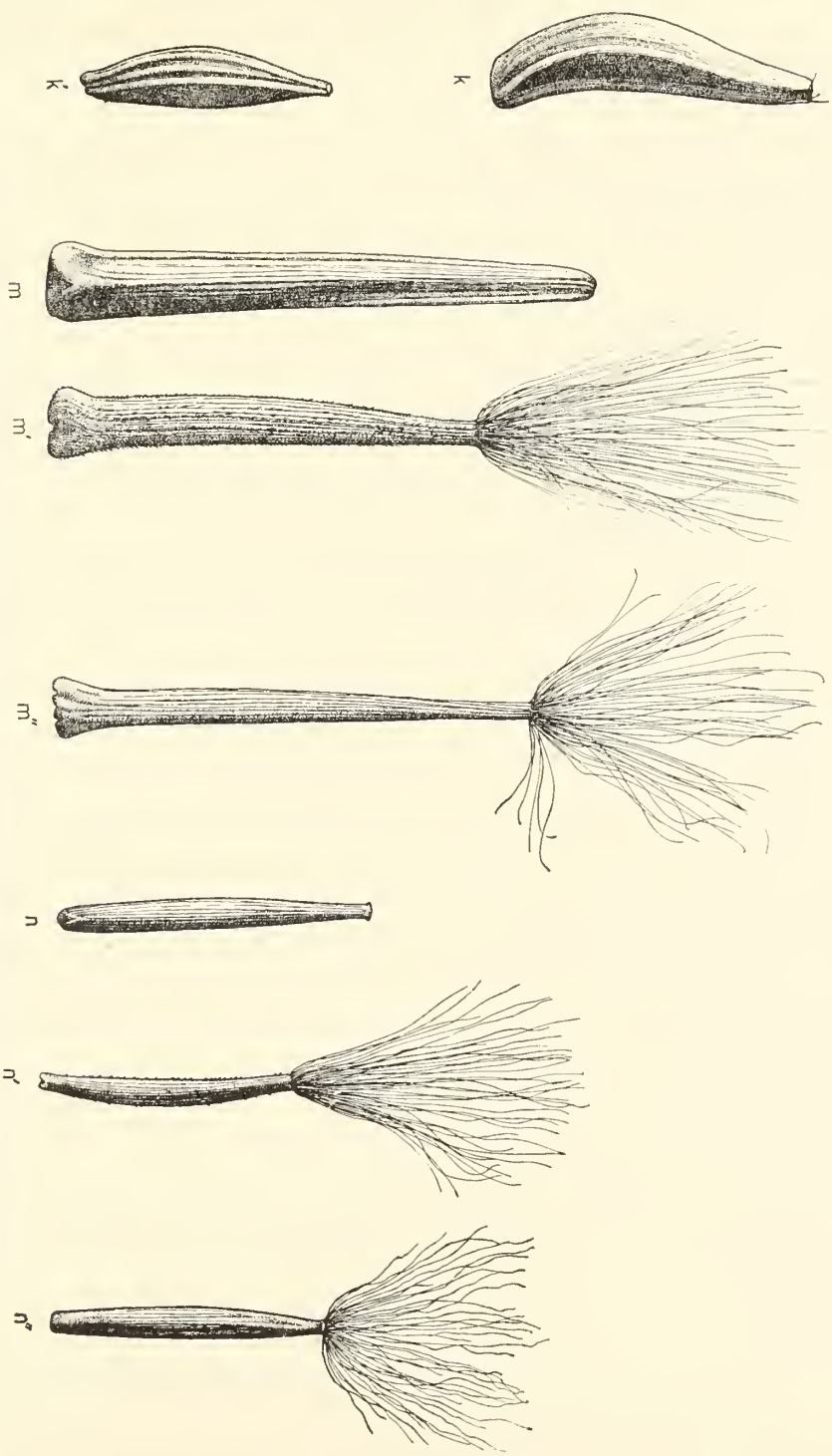

Fig. 4, *k*, *k'*, marginal and inner achenes of *Crepis Dioscoridis*; *m*, marginal and *m'*, *m''*, inner achenes of *C. palestina*; *n*, marginal and *n'*, *n''*, inner achenes of *C. pulchra* forma. × 7 *circa*.

grouped under Section II all having 5 pairs of chromosomes of similar size, while those under Sections III and IV have 4 pairs but differ somewhat in individuality. It is worthy of note that one character commonly used in distinguishing between these species, viz., the position assumed by the young flower heads before anthesis, whether erect or nodding, has been found to be too variable in the case of *foetida* to make it of diagnostic value.

In its dimorphous fruits, the inner ones beaked and the outer ones winged, *C. aspera* exhibits relationship with **Barkhausia** on one side and the *Dioscoridis* group on the other (cf. fig. 4, *k*, *k'*). Its chromosome group resembles those of the three **Barkhausia** species in having chromosomes of medium size, and it has been crossed with two of these species. But these hybrids exhibit very abnormal reduction phenomena, whereas hybrids between certain **Barkhausia** species (*vesicaria*, *Marschallii* and *taraxacifolia*) show normal pairing and reduction. Thus all the evidence indicates that *aspera* belongs in a class by itself. Furthermore, *amplexifolia*, which closely resembles *aspera* morphologically, also has 4 pairs of medium-sized chromosomes (p. 331).

Subgenus (*b*) is a heterogeneous group which is scarcely capable of satisfactory classification on the basis of fruit characters alone. Thus in the case of sections V, VI, and VII there is much stronger affinity, as indicated by comparative morphology, than would appear from Hoffmann's synopsis. In all three of the species concerned the inner involucral bracts of fructiferous heads are conspicuously thickened or much hardened. Then, too, *palaestina* has a combination of some of the distinguishing characters of the other two species, and yet it is in no sense an intermediate form such as might arise from hybridization. The flower heads in *palaestina* are large and showy, and the marginal fruits are enclosed within the inner involucral bracts, in these respects resembling *Dioscoridis*, while the inner fruits bear a strong resemblance to those of *pulchra*. Furthermore, the fruits in *pulchra*, contrary to Hoffmann, are sometimes of two distinct shapes, the marginal ones being flattened as in *palaestina* (cf. fig. 4). Without going into further details at this time, we may suggest that these three sections might well be combined into one. The chromosome groups of *pulchra* ($N=4$), *palaestina* ($N=4$), and *Dioscoridis* ($N=4$) are indistinguishable, and the F_1 of *pulchra* $\times$ *palaestina* is highly fertile.

Section VIII, **Aetheorrhiza,** must stand alone, at least for the present. While the inflorescence of *bulbosa* suggests strong relation-

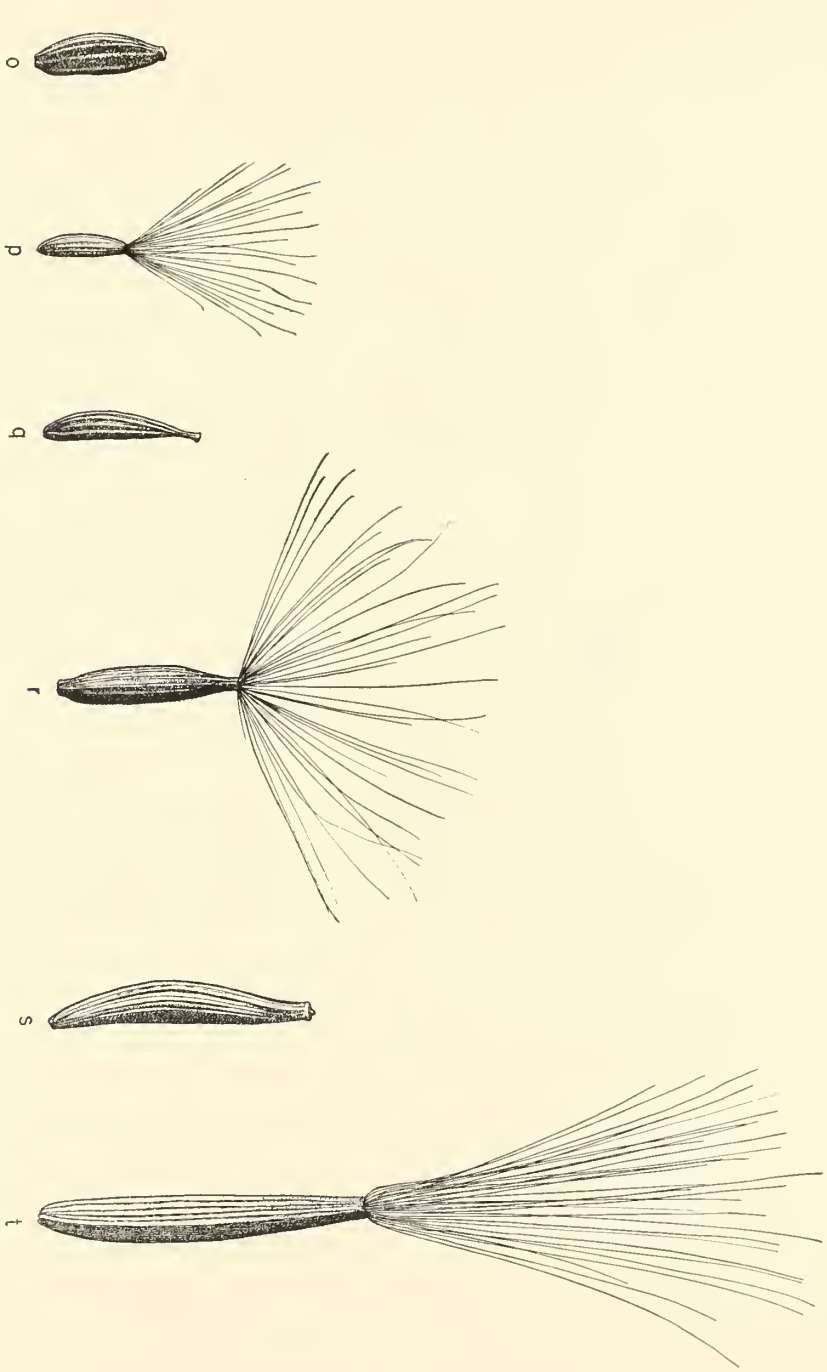

Fig. 5. Typical achenes of: *o*, *Crepis capillaris*; *p*, *C. parviflora*; *q*, *C. neglecta*; *r*, *C. tectorum*; *s*, *C. montana*; *t*, *C. biennis*. × 7 circa.

ship with *aurea*, this species is cytologically very different from all other species of *Crepis*, having 9 pairs of short chromosomes. The only species studied which it at all resembles in this respect is *japonica*, which has 8 pairs of chromosomes of similar size.

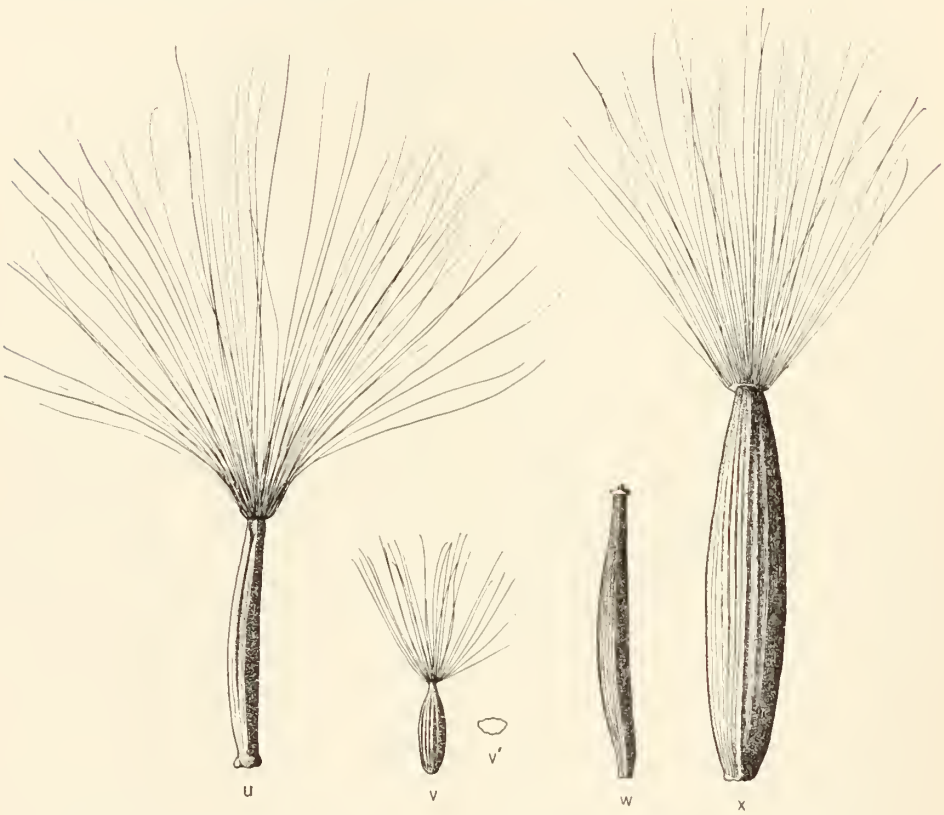

Fig. 6. Typical achenes of: *u*, *Crepis bulbosa*; *v*, *C. japonica*—*v'*, cross-section outline; *w*, *C. aurea*; *x*, *C. blattarioides*. × 6.5 *circa*.

Section IX, **Eucrepis**, contains six of our twenty-one species, and on the basis of fruit characters alone (cf. fig. 5) they comprise three groups, as follows: 1. *capillaris* and *parviflora*; 2. *neglecta*, *tectorum*, *montana*; 3. *biennis*. But if we consider habital and other morphologieal characters, they may be rearranged as follows: 1. *capillaris*, *parviflora*, *neglecta*; 2. *tectorum*; 3. *biennis*; 4. *montana*. Such an arrangement is of interest when considered in relation to the chromosomes of these species. It was noted (Mann, 1925) that the total length of the chromosome group in *capillaris* (N = 3) is practically the same as that of *neglecta* (N = 4), while *parviflora* (N = 4) appears to have a short chromosome added to a complex like that of *capillaris*. The chromosome group of *tectorum* (N = 4) could not be differentiated

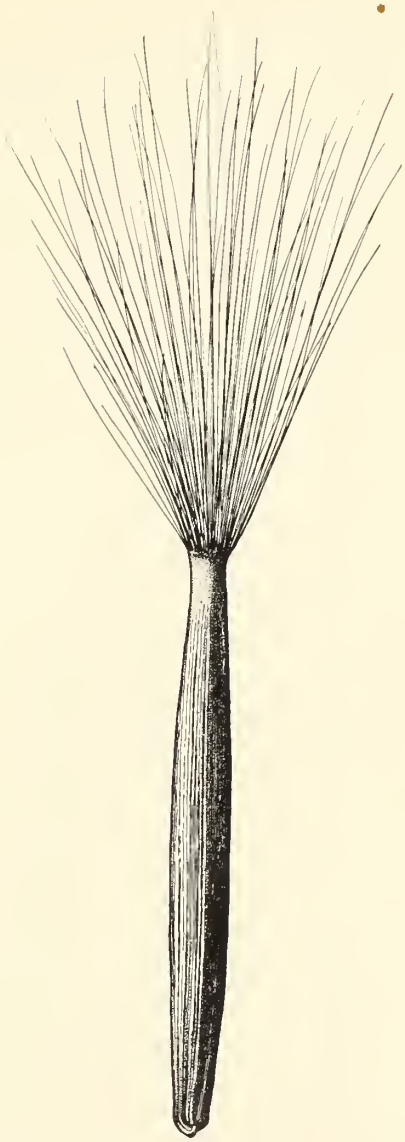

Fig. 7. Typical achene of: *y. Crepis sibirica.* × 7 *circa.*

from that of *taraxacifolia* in **Barkhausia,** but *biennis* (N = 20) and *montana* (N = 6) stand apart from all other species from the standpoint of chromosome number.

It should be observed that *C. neglecta* has long been a troublesome species to students of this difficult genus. In the Genera Plantarum (Bentham and Hooker, 1873) *neglecta* is considered as intermediate

between **Eucrepis** and **Lagoseries (Barkhausia)**; *parviflora* was given similar intermediate status, but this is manifestly an error. In the Flora Orientalis (Boissier, 1875) we find a statement which we translate as follows: "As the achenes gradually diminish into a short beak, it is doubtful whether this species belongs in **Eucrepis** or **Barkhausia**; it affords a connecting link between the two sections." Boissier places it under **Barkhausia**, presumably because the young flower heads assume a nodding position. The unreliability of this character has been pointed out. Moreover, recent taxonomists (e.g., Fiori, 1904) have placed *neglecta* in **Eucrepis**, where it seems to belong rather than in **Barkhausia**, as its fruits are variable in shape and even when they are beaked the beak is very short, as shown in figure 5*q*.

Section X, **Youngia**, is represented here by only one species, but contains several others, of which one is *fuscipappa* (p. 331). These comprise a very distinct group in certain morphological characters, insomuch that some authors have suggested placing it in *Lactuca*. But it is claimed (Bentham and Hooker, 1873; Hooker, 1882) that the species of this group (except two referred to *Lactuca* or *Ixeris*) resemble **Eucrepis** more closely than *Lactuca*, and that *japonica*, which is the type species of Cassini's genus, *Youngia*, does not differ much in floral characters from *C. parviflora*, a statement which is partially true, although a number of differences do exist. It was noted above that *japonica* ($N = 8$) resembles *bulbosa* in having very short chromosomes. It is the only species known in the genus with 8 *small* chromosomes (*japonica* chromosomes total about 93 units in length as compared with 137 for *fuscipappa*) and it was shown in Mann (1925) that considering chromosome size alone it might have been derived from *tectorum* **(Eucrepis)** by cross-division of all chromosomes. However, these two species are so widely different morphologically that such a derivation seems hardly possible. On account of the strongly flattened fruits in *japonica* (cf. fig. 6, *v*, *v'*), together with the other differences noted in Hoffmann's key and the small size of the chromosomes, one may advocate the recognition of Cassini's *Youngia* as a genus intermediate between *Crepis* and *Lactuca*. Cassini (1831) in the original diagnosis of *Youngia* states: "fruits oblong, more or less flattened, . . . absolutely beakless" . . . [genus] "not to be confounded with *Crepis* because of the flattened fruits." Further comparative study of shape of fruits and size of chromosomes will be necessary, however, before a final conclusion can be drawn.

TABLE 2

TENTATIVE CLASSIFICATION OF TWENTY-ONE SPECIES OF *Crepis*, ARRANGED FOR COMPARISON WITH HOFFMANN'S CLASSIFICATION SHOWN IN TABLE 1

B. Pappus bristles longer.
1. Inner or all the fruits long-beaked.
2. Fruits large, the inner ones 10–18 mm. long.
Sec. II. **Anisoderis.**
C. alpina, foetida, rubra (figs. 1 and 2).
2*. Fruits small, the inner ones 5–7 mm. long.
3. Fruits all similar.
Sec. III. **Barkhausia.**
C. bursifolia, setosa, taraxacifolia (fig. 3, *d, e, g*).
3*. Fruits of two shapes, the marginal ones winged.
Sec. IV. **Nemauchenes.**
C. aspera (fig. 3, *h, h'*).
1*. Fruits reduced at apex, but not beaked or only short-beaked.
4. Inner involucral bracts conspicuously thickened or hardened in fructiferous heads.
Sec. V. **(Gatyona, Cymboseris, Phaecasium.)**
C. Dioscoridis, palaestina, pulchra (fig. 4).
4*. Inner involucral bracts not much thickened or hardened in fructiferous heads.
5. Inner involucral bracts more or less spongy-thickened dorsally.
Sec. VI. **Eucrepis.**
C. capillaris, parviflora neglecta, tectorum, biennis, montana (fig. 5).
5*. Inner involucral bracts little or not at all changed.
6. Heads small, florets few, small.
Sec. VII. **Youngia.**
C. japonica (fig. 6, *v, v'*).
6*. Heads large, florets numerous, large.
7. Plant short-stemmed, scapigerous, scapes 1-headed, rarely 2–3 headed.
8. Rootstock stoloniferous, forming tubers.
Sec. VIII. **Aetheorrhiza.**
C. bulbosa (fig. 6, *u*.)
8*. Rootstock simple, non-tuberous.
Sec. IX. **Omalocline.**
C. aurea (fig. 6, *w*).
7*. Plant long-stemmed, erect, foliate.
Sec. X. **Soyeria.**
C. sibirica, blattarioides (fig. 6, *x;* fig. 7, *y*).

Section XI, **Catonia**, is defined by Hoffman as including species of at least two distinct groups, **Omalocline** Cass. and **Soyeria** Mann., represented among our species by *aurea* on the one hand and by *blattarioides* and *sibirica* on the other. In other words, he has used an ill-defined genus (Moench, 1794) as a catchall for species not already assigned to sections. This would be more evident if we were considering a larger number of species. Furthermore, *blattarioides*

and *sibirica*, although somewhat similar in both habital and fruit characters (see figs. 6, 7), are very distinct from each other in many respects and have the same general native and distributional habitats, all of which would indicate that they are not closely related species. The three species of **Catonia** studied differ greatly cytologically. *Aurea* (N = 5) is rather different in individuality from the other species with 5 pairs. *Blattarioides* (N = 4) has a chromosome group much like that of *tectorum*, while *sibirica* has 5 pairs of very large chromosomes resembling those of *Dioscoridis*, *pulchra*, and *palaestina*. Three other species in this section have been counted recently, but as no measurements have yet been made, they are not included in table 3 (see p. 331).

TABLE 3

TABULATION OF TWENTY-ONE SPECIES OF *Crepis* ACCORDING TO A TENTATIVE NEW TAXONOMIC GROUPING AND WITH REFERENCE TO NUMBER AND LENGTH OF CHROMOSOMES. (THE LENGTH VALUES REPRESENT AVERAGES FROM TEN DIFFERENT CELLS.)

	Number of Chromosome Pairs								
	1	2	3	4	5	6	7	8	9
Sec. II. **Anisoderis**									
alpina	26.2	21.3	14.5	13.1	12.2				
foetida	25.0	20.8	17.7	15.8	14.4				
rubra	29.4	23.9	18.5	16.2	14.9				
Sec. III. **Barkhausia**									
bursifolia	24.3	22.0	19.5	12.7					
setosa	22.3	17.8	14.0	9.1					
taraxacifolia	26.1	23.3	21.2	17.8					
Sec. IV. **Nemauchenes**									
aspera	23.9	21.5	19.7	17.5					
Sec. V.*									
Dioscoridis	35.9	29.3	24.9	19.3					
palaestina	34.1	27.0	24.6	21.2					
pulchra	36.7	30.6	25.5	19.3					
Sec. VI. **Eucrepis**									
capillaris	26.2	20.4	14.8						
parviflora	25.3	20.5	14.4	9.7					
tectorum	28.1	23.2	20.2	17.2					
montana	26.8	21.4	17.7	16.0	15.2	12.5			
biennis	(20 pairs) †								
Sec. VII. **Youngia**									
japonica	15.7	13.5	12.2	11.5	10.8	10.0	9.7	9.2	
Sec. VIII. **Aetheorrhiza**									
bulbosa	13.9	12.8	12.1	11.7	11.1	10.6	10.1	9.6	8.6
Sec. IX. **Omalocline**									
aurea	21.0	18.0	16.2	15.1	13.2				
Sec. X. **Soyeria**									
sibirica	41.9	32.4	27.6	23.2	18.5				
blattarioides	29.0	23.8	20.6	17.7					

* **Gatyona**, **Cymboseris**, and **Phaecasium** combined.

† Not measured; size range much like that of species in this group.

Our analysis of relationships among these twenty-one species, as based on comparative morphology, is summarized in table 2. This analysis is presented only in a tentative way, as an aid in the study of cytological evidence and a step toward the classification of the entire genus.

The correspondence of the new taxonomic grouping with chromosome number and size is shown in table 3.

Since the foregoing was written, the chromosomes have been examined in the following additional species of *Crepis*. The classification into sections is according to the tentative new arrangement shown in tables 2 and 3.

IV. **Nemauchenes**

C. amplexifolia (Godr.) Willk. N = 4 size medium

VI. **Eucrepis**

C. lyrata Froel. N = 6 size medium
C. mollis (Jacq.) Asch. N = 6 size medium

C. pygmaea L. N = 6 size medium

C. chondrilloides Jacq. N = 4 size large
C. Blavii Asch. N = 4 size large

C. ciliata C. Koch. N = 20 size medium

VII. **Youngia**

C. fuseipappa (Thw.) Benth. N = 8 size medium

IX. **Omalocline**

C. Hookeriana Ball. N = 4 size medium

X. **Soyeria**

C. conyzaefolia (Gouan) Dalla Torre N = 4 size large
C. tingitana Salz. ex Ball N = 5 size medium
C. paludosa (L) Mnch. N = 6 size large

With reference to the six species classified under **Eucrepis**, the first group of three *lyrata*, *mollis*, and *pygmaea*, must be grouped with *montana* on the basis of morphology, and they have similar chromosomes. The next two, *chondrilloides* and *Blavii*, represent a subdivision of **Eucrepis** not previously studied and are very distinct from other members of **Eucrepis**. Lastly *ciliata* is certainly in **Eucrepis**, and its chromosomes indicate relationship to *biennis*, to which species there is considerable resemblance in the rosettes of our immature plants. Evidently **Eucrepis** is too heterogeneous a group to be retained as a section, and in the taxonomic revision of the genus which is now in preparation it will become a subgenus containing several sections.

It is evident that, generally speaking, there is a definite correspondence between the taxonomic position of the species studied and their chromosome number and especially with chromosome size, and that the new taxonomic grouping increases this correspondence. It is almost perfect in Section II, and in Section III (cf. table 3), and the species that stand apart in the classification also differ markedly from the rest in either size or number of chromosomes (Sections V, VI, and VII). It will be noted that Section III and Section VI contain species with similar chromosome numbers and sizes, *parviflora* and *setosa* having very similar size differences, as do also *taraxacifolia* and *tectorum*. It would seem worth while to test these groups by means of species-hybridization. Sections VII and VIII as compared with Sections V and X exhibit the most extreme differences in chromosome size.

LITERATURE AND DISCUSSION

The numerous summaries of chromosome numbers which have appeared in recent years clearly indicate that there is some parallelism between chromosome number, size, and shape and relationship in the plant and animal kingdoms. In general, members of the same genus usually have similar chromosome numbers. In the Liliaceae, for instance, each genus has a characteristic number of chromosomes. On the other hand, in wheat, instead of exact numerical correspondence within the genus, the species fall into three groups with respect to chromosome number (Sakamura, 1918), einkorn having 7, emmer 14, and vulgare 21 pairs of chromosomes. These groups also differ from one another in susceptibility to rust, serological relations, and morphology (Sax, 1921). Thus in the genus *Triticum* the most similar species are most alike in chromosome number. Winge (1917, pp. 166–168) cites an interesting case from the Compositae. Species were described as having 8, 9, 14, 16, 18, 24, 27, 32, 36, and 45 pairs. When these species were classified by tribes, the numbers formed two series with 8 as the ground number for the Heliantheae, and 9 for the Anthemideae. Marchal (1920) recently noted that the species of the genus *Campanula* which belong to the section Medium have N values of 17, 34, or 51, but finds that the other section of the genus fails to show a similar numerical seriation, including such N values as 8, 10, and 13. He suggests (p. 66) that "The results of the cytological study of species of section II [Rapunculus] tend to show that this grouping is much less natural and less homogeneous than the preceding."

McClung (1908), on the basis of observations on many genera of Orthoptera, says,

> Merely as a result of the study I have made of the germ cells I would have classified these insects into two groups, one having a complex of twenty-three chromosomes and the other of thirty-three. On the other hand, many taxonomists, from careful and minute examination of the external anatomy of these same species, had agreed in placing them into family groups which they call the Acrididae and Locustidae.

McClung (1917) has made an especially thorough study of the genera *Hesperotettix* and *Mermiria*, and has had the benefit of the coöperation of experts on the classification of the Orthoptera, with similar results.

Metz (1914, 1916) has shown that the Drosophilidae have rather similar chromosomes and that the species form several groups on the basis of their cytological characteristics. Metz and Lancefield (1922) state that the 13 species belonging to class A, of which *D. melanogaster* is an example, are scattered throughout the genus. The Drosophilidae are of especial interest from the standpoint of cytology and taxonomy, since something is known of the arrangement of genes within the chromosomes of several species, and it is therefore possible to compare the chromosomes from a genetical as well as a purely morphological viewpoint. Sturtevant (1921) says, "44 recessive mutant genes in 41 loci of *D. melanogaster* and 12 recessive mutant genes of *D. simulans* (in 12 loci) are also recessive in *melanogaster-simulans* hybrids." Some of these genes are found in each of the 4 chromosomes indicating that "The data from *D. simulans* show what was suggested by the other results and by much cytological data, that the constitution of a chromosome may be essentially the same in two different species." Both of these species belong to type A *cytologically* (Metz and Moses, 1923) and are closely related taxonomically. The evidence from *D. obscura* and *D. willistoni*, on the other hand, shows that the chromosomes which one would naturally suppose to be identical on the basis of purely cytological criteria are not the same genetically, since Metz and Lancefield (1922) state: "In the two species having V-shaped X chromosomes, then, yellow and scute are 'located' near the middle of the chromosome map, while in *melanogaster* with its short rod-like X chromosome, yellow and scute are on one end." Metz and Moses (1923) emphasize the importance of genetical evidence in any attempt to evaluate the significance of similarities or differences of a cytological type.

Lists of chromosome numbers also contain what appear to be many flagrant exceptions to the view that the species of a genus will be cyto-

logically similar. In fact, the summaries of Ishikawa (1916) and Tischler (1916, 1922) contain very few genera with either the same number throughout, or even a single ground number. Even in the Liliaceae certain species have been reported as having chromosome numbers different from that typical of the genus. Time and further work alone will tell how many of these exceptions are real and how many are due to error. At present few genera have been much studied, and even where a large number of counts have been published, the same error may appear in a whole series of observations. For instance, in both *Triticum* and *Rosa* numerous species were included in recent summaries as having 8 and 16 pairs of chromosomes. It has been shown by Sakamura (1918) and Sax (1918, 1921) for *Triticum*, and by Täckholm (1922) for *Rosa*, that 7 and not 8 is the ground number for both genera. Another very real source of error in any attempt to generalize from summaries lies in the fact that few cytologists are trained taxonomists. Our experience with *Crepis* indicates that seeds which are obtained from the most reputable sources may be incorrectly labeled, and, unless the seeds are grown and the plants classified, we cannot always be positive that they even belong to that genus, much less to the species to which the sender has attributed them. While lists of chromosome numbers include such errors as are indicated above and are, therefore, not suitable as a basis for very sweeping generalization, no one can doubt that chromosome number and, in some cases, size and shape, are good specific characters. We venture the prediction that chromosome number and size will sometime be given with taxonomic descriptions.

Crepis contains species with 3, 4, 5, 6, 8, 9, and 20 pairs of chromosomes; but 3, 6, 8, 9, and 20 are much less frequent numbers than 4 or 5, each of the former characterizing only one of the twenty-one species represented in table 3. A similar condition has been described for a closely related genus, *Lactuca* (Ishikawa, 1921), most of the species having 5, 8, 9, or 12 as the haploid number, while single species have 7, 16, or 24. It is especially interesting that Ishikawa finds that his grouping of species according to chromosome number and size corresponds very strikingly with the taxonomic classification of Nakai (1920). In *Lactuca*, as in *Crepis*, great differences in chromosome size exist, and because of this and the numerical differences, Ishikawa is inclined to think that *Lactuca* is really an assemblage of genera. It is particularly interesting that two varieties of *L. dentata* have 12 pairs, while one has 7 pairs of chromosomes.

Crepis senecioides Delile, a native of Egypt, is a species of peculiar interest because its fruit is definitely flattened, although not so much so as in the more extreme types of *Lactuca*, and it lacks the thin lateral margin (fig. 3, *f*, *f'*), while on the basis of its involucre, number of florets per head, and habit it does not fit into any of the sections of *Lactuca* provided by Hoffmann in the Pflanzenfamilien. Furthermore, it has four pairs of small chromosomes and produces sterile hybrids when crossed with *C. parviflora* and *C. vesicaria*. Thus we find fairly close relationship between what simulates *Lactuca* in achene shape and certain species of *Crepis*. This evidence is not unique, however, as there are other points at which the two genera meet. Nakai, for example, found it necessary to choose between the alternatives of either recognizing *Ixeris*, *Paraixeris*, and *Crepidiastrum* as distinct genera or combining *Crepis* and *Lactuca*. For the present, we are inclined to consider *C. senecioides* as *Crepis*, but it is highly desirable that critical comparison of the fruits be made between *senecioides* and similar *Crepis* species as well as between *senecioides* and the North African species of *Lactuca*, and that chromosome counts of the latter be obtained. We have indicated one such comparison in the drawing of *C. bursifolia* (fig. 3, *g*, *g'*).

A group of forms which have usually been treated as distinct species, viz., *Crepis vesicaria* L., *C. taraxacifolia* Thuill., *C. Marschallii* F. Schultz, and *C. myriocephala* Coss. et DR., may be considered as one species for the following reasons: (1) They are closely similar morphologically, and their close relationship has been recognized by several taxonomists. (2) They have nearly identical chromosome groups. (3) They intercross freely and produce highly fertile hybrids. That these should be considered as subspecies of one species rather than as varieties is indicated by the following facts: (1) All except one, *taraxacifolia*, which is probably the oldest phylogenetically, occupy distinct geographic areas. (2) All are highly variable, and *taraxacifolia* is really polymorphous. However, as no changes in nomenclature are proposed in the present paper, we shall continue to use the binomials in what follows.

A summary of the data recently presented by Bleier (1925) and Karpetchenko (1925) shows that in *Trifolium* section **Chronosemium***

* Greene (1897) discusses at length the evidence for retaining the genus *Chrysaspis* instead of treating it as a section **(Chronosemium)** of *Trifolium*. He says: "And since Linnaeus' time there have been a number of open protests, and by most able botanists, against the treating of the Hop Trefoils as congeneric with such plants as *Trifolium pratense* and its allies. Systematists of no less renown than Lamarck and Desfontaines referred the plants to *Melilotus* rather than *Trifolium*."

contains species with 7 or 14 pairs of chromosomes, while **Enamoria** and **Galearia** consist of species with 8 or 16 pairs, except for *T. glomeratum* which has 7 pairs; whereas **Lagopus** contains species with 7, 8 or a large number of pairs, possibly 48–49. Bleier presents some evidence that differences in nuclear volume and in chromosome size occur in the genus. The cases of *Trifolium*, *Campanula*, *Lactuca*, and *Crepis* are alike in that, while many correspondences have been found between chromosome number and classification, some exceptions still exist which require further study. Even within **Eucrepis**, however, which shows a remarkable diversity of chromosome numbers, morphological resemblances appear within the section which are correlated with similarity of chromosome number and size.

In the genus *Senecio*, Afzelius (1924) reports a high degree of homogeneity within the genus as indicated by close conformity to the numerical series, 5, 10, 20, 30; also in most of the sections, as only one of the eight sections contains species of different numerical rank. However, as the species he has studied are mostly from the Old World, the situation within the genus as a whole may yet be found to differ considerably.

In *Carex*, Heilborn (1924) has recently reported that species exist with 9, 15, 16, 19, 24, 26, 27, 28, 29, 31, 32, 33, 34, 35, 36, 37, 38, 40, 41, 42, and 56 as haploid numbers. Related species show some numerical similarity, although this is by no means so striking as in *Lactuca*.

Crepis also contains a series of chromosome numbers like that reported for *Carex*, 3, 4, 5, 6, 8, 9, and 20 pairs. Most of the species with 3, 4, 5, 6, and 20 pairs have chromosomes similar in size, although some 4- and 5-paired species have chromosomes that are much larger than is usual in *Crepis*, in so far as it has been studied cytologically. Two of the three species which we have found with 8 and 9 pairs have much smaller chromosomes than is usual in the genus. It was noted above that the section **Youngia** might be removed from *Crepis*. If this is done we shall lack species with 8 pairs. It is noteworthy that **Eucrepis** contains species with 3, 4, 5, 6, and 20 pairs. Navashin (1925*b*) and Collins and Mann (1923) found evidence that polyploidy occurs in *Crepis*, but it was pointed out by Mann (1925) that some other type of chromosome multiplication must account for the origin of most of the species which we have studied. Non-disjunction was first suggested as a source of the chromosome differences observed by Rosenberg (1918); and, whereas this cannot account for all the differences, it may be the most important factor. In any case it certainly

is the most probable method which we know occurs. It should be emphasized in all such discussion, however, that there is *no known case of a stable combination of chromosomes which has been observed to originate in this way.* Similarly, no case of changed individuality of the chromosomes which would account for stable types like *C. setosa*, *neglecta*, and *parviflora* has been reported to have occurred experimentally. Chromosome fragmentation is known to occur following trisomy, but whether such types ever become stabilized with a pair of fragments added to the normal specific complex, or whether a chromosome complex can lose a considerable section of a pair of chromosomes and the plants lacking this part be viable and fertile, is unknown. Our strain of *C. Marschallii* is peculiar in that, when we obtained it, certain plants contained 9 chromosomes in the root-tip cells, comprising the usual complex for the *vesicaria* group of species plus a very short unpaired chromosome. The source of this small extra chromosome is quite uncertain, although it is known to be an addition to the complex. Navashin (1925) presented a figure of *C. Marschallii* that is like *vesicaria* and lacks the small chromosome. Some of our 9-chromosome *Marschallii* plants were very fertile, and among their progeny one at least has two such small chromosomes. This matter is being studied further and will be reported upon separately. Should such a plant be fertile, we might understand how such differences in chromosome groups could arise in a genus.

Navashin (1925*a*) has emphasized the importance of minute "*Trabanten*" or satellites attached to the tips of certain chromosome pairs in *Crepis* species. He believes that shape of chromosome and the presence or absence of satellites is "*weit wichtiger für die Charakteristik des Kernes bzw. der Art, als die Zahl der Chromosomen und deren Dimensionen sind.*" He groups together in class "D" all chromosomes having satellites although in *C. Dioscoridis*, one of 19 length units bears the satellite, while in *C. parviflora* he finds it upon one of about 10 length units. But in our material, which was fixed in C. A. U., *Trabanten* were not always present, and sometimes resembled the strands and masses of nucleolar material which are frequently found being extruded from the chromosome plate. Consequently size, which is relatively far less variable and more easily evaluated, was selected as the best criterion of relationship, and it has thus far proved a very good one as tested by species-hybridization. That shape relationships may help in differentiating two pairs of chromosomes of the same size in certain species of *Crepis* is clearly indicated by Navashin's figures,

but the relative importance of size and shape as indicators of relationship between species can be tested only by species-hybridization and genetic analysis. Probably both modes of attack will sometime prove useful, but thus far they have not given us clues to relationship which could not be determined by comparative length alone. Our material, like that of Navashin, shows *Trabanten* attached to the shortest chromosome in both *tectorum* and *Marschallii*, species which are widely separated in all classifications. This is very disappointing, since one might have hoped that they could be differentiated thereby. It seems evident from our studies that if Navashin were to make comparative measurements of the chromosomes, he might change his estimate of the chromosome homologies in the species which he studied.

Corrections in Nomenclature in Part I

In the preceding paper (Mann, 1925), the following corrections should be made:

For *breviflora* Delile read *senecioides* Delile.

For *grandiflora* Tausch read *conyzaefolia* (Gouan) Dalla Torre.

For *Sieberi* Boissier read *montana* d'Urville.

SUMMARY AND CONCLUSIONS

1. Taxonomically considered, the genus *Crepis*, as it stands at present, is a heterogeneous assemblage of distinct but related groups of species. The sections recognized by Hoffmann and their classification by him are not wholly satisfactory on the basis of comparative morphology alone. A more satisfactory classification of the species under consideration, which reduces the sections from eleven to ten and regroups certain species, is suggested, and the cytological evidence is considered in relation to the new grouping.

2. From the standpoint of cytology as well, the genus *Crepis* must be considered as heterogeneous. Similarity of chromosome size seems to be a better criterion of relationship than number alone, although closely related species usually have the same numbers of chromosomes. Most of the cytological heterogeneity is confined to the sections **Eucrepis** and **Catonia** of Hoffmann's classification. The former is found to be too heterogeneous both taxonomically and cytologically to be retained as a section, and certain new subgroupings are needed within it. **Catonia** also requires some drastic changes. It is hoped that further study will reveal natural subgroups within **Catonia**; also

that it may throw light on the origin of chromosomal differences in *Crepis*. Further research on species hybrids is in progress and should throw considerable light on problems of relationship within the genus.

3. Differences in chromosome dimensions are found among the species of this genus. We note especially (*a*) differences in size of all the chromosomes; (*b*) similarity in size of most of the chromosomes and differences in others. If **Youngia** be omitted, there remains only one species, *C. bulbosa*, having all the chromosomes smaller than is usual for the genus. At present we have this species in a section by itself, but its ultimate classification awaits further study. Of the three species of type (*b*), in which certain chromosomes are much shorter than is usual in the genus and the others are similar in size, *C. neglecta* and *C. parviflora* are provisionally classified in **Eucrepis**, while *C. setosa* is in **Barkhausia**.

4. It is noted that certain species having similar chromosome sizes, particularly *C. tectorum* and the *vesicaria* group (including *taraxacifolia*, *Marschallii*, and *myriocephala*), are classed respectively in **Eucrepis** and **Barkhausia**. These facts may indicate either close relationship between the two sections or that similar changes in the chromosomes have taken place independently in the two groups. For the present we favor the latter assumption.

5. This study was undertaken partly for the purpose of testing the cyto-taxonomic method in a genus favorable for such research. As the work progresses we are becoming more and more impressed with the value of this method, and it is our intention to extend it to include as many species of *Crepis* as can be obtained and cultivated at Berkeley.

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